Insights for Robotic Design From Studies of the Control of Abdominal Position in Crayfish

DAVID L. MACMILLAN* AND BLAIR W. PATULLO

Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia

Abstract. Studies of the control of position and movement of the abdomen of crayfish illustrate a number of features of invertebrate sensory-motor systems that have implications for their use to inform robotic design. We use the abdominal slow extensor motor system to illustrate three of them here: first, the way in which a behaviorally flexible length-servo device can be achieved with very few elements; second, the importance of knowledge of the biological and behavioral context in which the elements operate; third, that design solutions resulting from natural selection have been constrained by the previous evolutionary history of the animal, which can affect the outcomes in ways that may not be immediately apparent in a design context.

Introduction

Crayfish, and other crustaceans with tubular bodies, have proprioceptive structures called muscle receptor organs (MROs) spanning the articulations between the segments (Alexandrowicz, 1951). Each MRO signals the relative position and movement of the two segments to which it attaches. Since the discovery of MROs, many different aspects of their biology have attracted the interest of neurobiologists (Fields, 1976; Macmillan, 2001). In this paper we combine data from the literature with insights from our current work on crayfish to highlight three aspects of MRO

biology with interesting implications for biologically inspired robots: that arthropods achieve complex behavioral outcomes with few neurons, that assumptions derived from reduced preparations or parts of animals need to be tested in biologically meaningful situations in intact animals, and that it is important to have an appreciation of the impact of natural selection when examining biological solutions to engineering design problems.

The abdomen, or tail, of the crayfish is composed of five similar, articulated tubes connected by simple lateral hinges that permit movement only in the pitch plane (Fig. 1A). The connection between the thorax and the first abdominal segment is different. It is surrounded by strong, flexible membranes enclosing stout muscles anchored deep within the thorax. In addition to movement above and below the horizontal line of the body, the joint allows limited rotation in the roll and yaw planes so that it acts as a limited-range universal joint. The functional outcome is flexibility of position and movement at the other end of the tail where the biramous appendages (uropods) of the sixth abdominal segment, together with the telson, form a tailfan (Fig. 1A). The tailfan elements elevate and depress and also slide over each other laterally so that the whole tailfan can vary in size and can change shape from paddle to scoop. This flexibility at the end of the hinged lever that is the tail permits the animal to modify the direction and magnitude of the forces generated when it flexes and extends its tail for swimming and balancing. The arrangement presents an interesting case study for biological solutions to problems associated with the dynamics and control of multi-jointed levers.

The muscles controlling the movement of the tail are divided into four matching sets: the slow and fast flexors and extensors. The fast flexors ventrally and fast extensors dorsally occupy most of the abdominal cavity (Fig. 1B) and are responsible for escape tail flip behavior and swimming. Although related developmentally to their segment of ori-
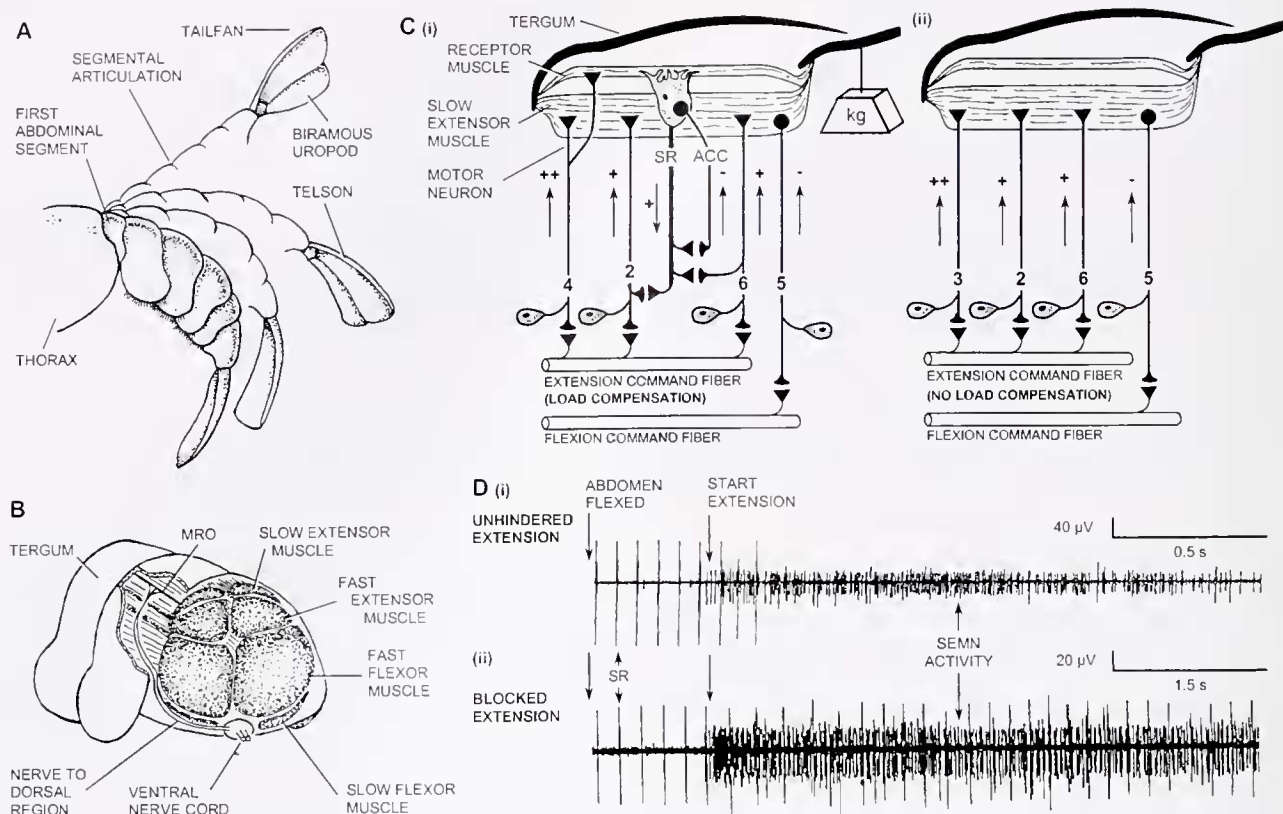
Figure 1. (A) Lateral view of the crayfish abdomen showing the changing position and shape of the segments and tailfan during a movement from a mid-flexed position to full extension. The joints between the abdominal segments permit movement only in the pitch plane, whereas that between the thorax and first abdominal segment permits movement in pitch, roll, and yaw planes. (B) Diagram of a section of the abdomen showing placement of the main muscle blocks in cross-section and the ventral nerve cord and its connection with the MRO in one segment. (C) Summary of the nerve-muscle connections operating when (i) the SEMN4 program is operating and the SR load-compensation loop can be recruited, and (ii) the SEMN3 program is operating and the SR load-compensation loop is not recruited. Triangles and circles represent excitatory and inhibitory synapses respectively. (D) Pattern of activity of the SEMNs and SRs recorded from the dorsal nerves during a platform drop extension (i) in abdominal segment 4 when the movement is unhindered, and (ii) in abdominal segment 2 when a rod and mechanical stop prevent straightening of the joint spanned by this MRO throughout the extension taking place at the other abdominal joints. Note that these recordings are displayed on different time and amplitude scales.

gin, they are organized into the overlapping muscle spirals familiar to lovers of lobster as a gourmet delicacy. Common connective tissue strands that run the length of the tail ensure that they act as a coordinated unit when delivering their power. The slow flexor and extensor muscles, which are responsible for slow movements and postural adjustments, lie ventrally and dorsally respectively, in thin sheets external to the bulk of the fast muscles and immediately beneath the surface of the exoskeleton (Fig. 1B).

The Remarkable Parsimony of Arthropod Neuromuscular Control

Vertebrates achieve fine control in muscles primarily by having large numbers of motor units that can be recruited sequentially and, to a lesser extent, by heterogeneity of their nerve and muscle. The pools of motor neurons employed by vertebrates to achieve fine control of their muscles need space that the small-bodied arthropods do not have. Arthropods achieve comparable levels of control with far fewer neurons (insects typically have only two or three motor neurons per muscle and crustaceans have up to five or six). They achieved this reduction in part by employing nerve-muscle combinations ranging in their contraction characteristics from slow and gradual to fast and twitching, and partly by evolving motor neurons that inhibit muscle contraction in parallel with the more familiar ones that cause contraction. These developments massively increase the possibilities for a continuously graded range of contraction outputs

and for the integration of excitatory and inhibitory inputs throughout the control mechanism without a concomitant increase in the number of motor neurons. These ingenious and effective ways of reducing the number of neurons could well be of interest in robotic design. The fact that variations of these arrangements are found throughout the arthropods suggests that they evolved early. Comparative studies show that they have not necessarily been advantageous in all subsequent behavioral situations and provide interesting insights into ways in which design flexibility is achieved from a base model constrained by its evolutionary history to very few motor neurons (Paul, 1991).

Each of the segmental muscle groups in the crayfish is innervated by just six motor neurons per segment; these are conventionally numbered from 6 to 1 in descending order of axonal diameter (Fields and Kennedy, 1965; Fields, 1966; Drummond and Macmillan, 1998a,b). Each displays particular functional characteristics exemplified by the slow extensor sensory-motor system about which most is known and on which we will concentrate here. Slow extensor motor neuron 6 (SEMN6) is the largest motor neuron in the group. It innervates predominantly the fastest fibers in the slow extensor muscle. At low firing frequencies it produces large membrane responses that facilitate rapidly and sum when the frequency of stimulation is high to produce strong, twitch-type contractions. SEMN5 is slightly smaller in diameter than SEMN6. Its effect on the muscle potential is inhibitory—that is, it produces ionic permeability changes that hyperpolarize the muscle membrane and move its excitability away from the threshold for contraction, thereby modifying the nature of the contraction produced by exciter activity. SEMN4 and SEMN3 are almost indistinguishable in size and innervate almost the same population of slow extensor muscle fibers throughout all the slow extensor muscle bundles. They both evoke small to medium-sized responses that show modest facilitation and sum readily to produce smooth contractions at higher frequencies. SEMN2 is a small neuron that innervates almost all the slow extensor muscle fibers. Its activation produces small, non-facilitating muscle responses that sum to produce strong, slow muscle contractions at high frequencies. SEMN1 is a neuron of about the same size, but its muscle potentials and contractions are small, so its physiology is not well documented. From a design perspective, these elements provide for a full range of control options in the slow-fast and fine-coarse spectra while preserving remarkable component economy.

This brief outline of the innervation of this major muscle series shows that although the slow extensors in each segment are controlled by bilateral pairs of only six motor neurons, the flexibility inherent in their properties and patterns of innervation together with the trick of peripheral inhibition provide the same sort of flexibility available to multi-neuronal vertebrate equivalents. SEMN6 can be used

for twitch or brief, strong contractions; SEMN4 and SEMN3 for rapidly developing and decaying smooth contractions; and SEMN2 for slowly developing, sustained smooth contractions. Activation of SEMN5 reduces the contractions evoked by any contemporaneous exciter activity and also returns the membrane potential of slower fibers to their resting level more rapidly following slow exciter activity, thereby increasing the rate of muscle relaxation.

What do we know about how the potential flexibility of this parsimonious arrangement is employed by the crayfish? To answer this question we have to make a brief side trip into the sensory biology of the MROs.

The Sensory Biology of the Muscle Receptor Organs

A pair of MROs span the articulations between adjacent abdominal segments on each side of the body (Fig. 1B). Each pair of MROs has two stretch receptor (SR) neurons, a large, high-threshold phasic neuron and a smaller, low-threshold, tonic one. These respond to changes in the tension of a small, innervated receptor muscle strand in which they are embedded. Because the muscle spans the articulation, the SRs monitor the position of the abdominal segments relative to one another, and because the strand is innervated, their level of activity, or set point, can be adjusted from the central nervous system. SR activity levels can also be adjusted by the axons of inhibitory cells called accessory motor neurons (ACC) that synapse directly onto the SR surface and inhibit or delay sensory spike activation (Fig. 1Ci). The receptor muscles lie in parallel with the slow extensor muscle but are not powerful enough to assist with joint movement. These elements and their arrangement suggest those an engineer might employ in designing a servo-controlled load-compensating device (Fig. 1Ci).

Analysis reveals that this sophisticated and economical arrangement of elements has the potential to deliver flexible abdominal control. Experiments on semi-intact and isolated abdominal preparations (mainly in *Procambarus clarkii* and *Cherax destructor*) reveal a number of connections and reflexes involving the tonic SRs and the motor neurons in the local and adjacent segments (Fields, 1976; Drummond and Macmillan, 1998a; summarized in Fig. 1C). Activation of the tonic SR excites ACC, which inhibits the sensory neuron itself (Eckert, 1961)—a negative feedback loop that radiates weakly to adjacent segments. Functionally, this loop provides a classic myotatic reflex: it damps small displacements of the joint by externally imposed force, and it may also damp SR reflex loops. The tonic SR also excites the ipsilateral SEMN2 in its own segment, the motor neuron that produces slow sustained contractions in most of the slow extensor muscle fibers. This is the basis of a "resistance reflex." If the joint is flexed so that the tonic SR is activated, it will excite SEMN2, which will fire and extend

the joint until the receptor is unloaded and stops firing (Fields, 1966; Fields *et al.*, 1967).

Another important feature of the neuromuscular wiring is that SEMN4 innervates both the slow extensor muscle and the receptor muscle so that both could contract synchronously when it is activated. This relationship spawned a hypothesis about the way in which feedback could operate on the tonic sensor to produce different behavioral outputs. If central drive for extension included SEMN4, the tonic SR would not be activated during the extension because the MRO receptor muscle would contract with the main extensor muscle. If the movement met with resistance and the rate of extension slowed, the receptor muscle would continue to contract at the rate determined by the central drive onto SEMN4. Rising tension in the receptor muscle would activate the SR to recruit SEMN2 or increase its firing rate until the receptor was again unloaded. The circuitry is also configured to permit the same movement without activation of SR-mediated load compensation (Fig. 1Cii). If the central drive for extension were directed through SEMN3 rather than SEMN4, the same muscle fibers would be activated but the receptor muscle would not contract during the movement, and thus the length-servo loop would not be activated. This is how this sensory-motor cluster appears to operate in isolated *C. destructor* preparations. The SEMN3 and SEMN4 are not active together during spontaneous activity (Drummond and Macmillan, 1998a), and SEMN6 only fires at the peak of bursts of spontaneous activity in SEMN4 or SEMN3. SEMN2, on the other hand, can be recruited at any stage during ongoing activity in either unit. The pattern of firing in SEMN5, the inhibitor, suggests that it is used both to inhibit extensor contractions—for example, by firing during flexor muscle activity—and also to move the contractions due to repetitive activation of the intermediate fast-slow units SEMN3 and SEMN4 towards the more phasic end of their spectrum by suppressing their tendency to sum responses. In summary, there is ample potential for remarkable functional flexibility, notwithstanding the small number of neurons involved.

The Operation of the Receptors in Freely Behaving Animals

The finding that circuitry is capable of producing outputs predicted by a hypothesis and that it does so in non-behavioral, dissected preparations is a valuable step towards understanding how it might function, but from a robotics viewpoint, observation of its function and role in the biological and behavioral world of the animal is essential. We therefore set out to examine how the MROs and SRs operate in intact, freely behaving animals. Using surface markings to locate the position of the MROs, we implanted fine wire electrodes to make long-term recordings from the SRs and the SEMNs in *C. destructor* (McCarthy and Macmillan,

1999a,b). When an immersed crayfish loses contact with the substrate, it extends its abdomen so that it falls in a balanced, feet-down attitude, ready to walk as soon as it lands. This type of extension movement can be evoked by dropping a hinged platform on which the animal is standing (Larimer and Eggleston, 1971). The behavior was therefore dubbed "a platform-drop extension." The outcome of our platform-drop experiments provided a sharp reminder of the importance of evaluating hypotheses derived from reductionist analysis by testing them in the real world of the animal. This caution is particularly germane if the interpretations are to inform or lead robotic design.

In *C. destructor*, the tonic SR was invariably active when the animal was in the resting position with its abdomen curled beneath the body. The neuron fired very regularly, with a frequency around 16 Hz (Fig. 1D), the actual rate being slightly higher or lower depending on the whether the abdomen was more or less flexed. Activity was seen in the SEMNs as soon as the platform was dropped to initiate the extension, but by the time extension movement was apparent to an observer, the SR had ceased firing (Fig. 1Di). This result surprised us because previous results from other species suggested that the SR would fire throughout the extension (Sokolove, 1973). It could, however, be explained in system terms if the SR falls silent because the receptor muscle and the working extensor muscle are contracting at about the same rate but with the straightening of the joint just slightly leading the contraction of the receptor muscle. To test this possibility, we recorded from the SR in a segment that was prevented from straightening at all because of a small rod inserted between two acrylic plastic blocks glued either side of the joint. In this situation, the expected load compensation occurred, as evidenced by the increase in output by the motor neurons compared with their firing rates in the unblocked situation (Fig. 1Dii). It was not, however, due to recruitment of the local MRO, because the rate of firing in the SR remained constant throughout the extension movement (Fig. 1Dii). Some other receptors must have been responsible. This outcome was also unexpected because of earlier indications from other species that the MROs might be involved in load compensation (Sokolove, 1973). We hypothesized, however, that the reason the SR load-compensation pathway is not selected for platform-drop extensions is that, in this situation, the animal uses the SEMN3 mode rather than the SEMN4 one. Extension in this context is part of a stability or balancing behavior that gives the body a parachute-like profile. In the unlikely event that the animal encounters resistance during its fall through the water, it can then change posture to prepare for defense or other behaviors, some of which may involve the SR-SEMN4 load-compensation loop. To test this hypothesis, we used our ability to record from freely moving animals to study the activity of the SRs and SEMNs during a range of other behaviors, including some—such as the extension that

accompanies the assumption of the defense posture—in which load compensation, possibly mediated by the SR loop, could be expected to occur. As yet, we have found no behavior in *C. destructor* in which the SR-SEMN4 loop is activated when SEMN output increases in response to increased load (Patullo *et al.,* 2001).

Behavioral Context—the Key to Design Insights

The message is clear. This elegant circuitry works in a dish and we can see ways in which it could be employed to control movement, but we do not yet know enough about the biology to understand completely how the animal uses the components. Such understanding is necessary if we are to exploit the full potential of this sensory-motor system to inform our design of fine movement control devices with component economies suitable for robotic applications. It may be that the capabilities of the circuitry are not primarily targeted at the control of slow, postural movements. We have evidence, for example, that the SRs are cyclically active during non-giant swimming and that interference with their function alters such movements (Daws, McCarthy and Macmillan, unpubl. data). It is also possible that the normal function of the local feedback loops is evident only when they are operating as part of a concatenated chain involving the whole of the jointed abdominal lever. In support of this possibility is evidence that the cord stretch receptors have different effects on motor output when they are activated in groups rather than singly (Drummond and Macmillan, 1997). The study of abdominal movement in these animals has already provided insights into the way in which fine control can be achieved with very few elements and the necessity of fully understanding the context in which control mechanisms are to function. It promises many more as we achieve a better understanding of the biology.

Acknowledgments

Literature Cited

Alexandrowicz, J. S. 1951. Muscle receptor organs in the abdomen of *Homarus vulgaris* and *Panulirus vulgaris. Q. J. Microsc. Sci.* **92:** 163–199.

Drummond, J. M., and D. L. Macmillan. 1997. Cord stretch receptors of the Australian freshwater crayfish, *Cherax destructor. Soc. Neurosci. Abstr.* **23:** 1569.

Drummond, J. M., and D. L. Macmillan. 1998a. The abdominal motor system of the crayfish, *Cherax destructor.* 1. Morphology and physiology of the superficial extensor motor neurons. *J. Comp. Physiol. A* **183:** 583–601.

Drummond, J. M., and D. L. Macmillan. 1998b. The abdominal motor system of the crayfish, *Cherax destructor.* 11. Morphology and physiology of the deep extensor motor neurons. *J. Comp. Physiol. A* **183:** 603–619.

Eckert, 1961. Reflex relationships of the abdominal stretch receptors of the crayfish. 1. Feedback inhibition of the receptors. *J. Cell. Comp. Physiol.* **57:** 149–162.

Fields, H. L. 1966. Proprioceptive control of posture in the crayfish abdomen. *J. Exp. Biol.* **44:** 455–468.

Fields, H. L. 1976. Crustacean abdominal and thoracic muscle receptor organs. Pp. 65–114 in *Structure and Function of Proprioceptors in the Invertebrates,* P. J. Mill, ed. Chapman and Hall, London.

Fields, H. L., and D. Kennedy. 1965. Functional role of the muscle receptor organs in crayfish. *Nature* **206:** 1235–1237.

Fields, H. L., W. H. Evoy, and D. Kennedy. 1967. Reflex role played by efferent control of an invertebrate receptor. *J. Neurophysiol.* **30:** 859–874.

Larimer, J. L., and A. C. Eggleston. 1971. Motor programs for abdominal positioning in crayfish. *Z. Vgl. Physiol.* **74:** 388–402.

Macmillan, D. L. 2001. The abdominal muscle receptor organ of crayfish and lobsters: old models new challenges. In *Frontiers in Crustacean Neurobiology.* Springer, Berlin. (In press).

McCarthy, B. J., and D. L. Macmillan. 1999a. Control of abdominal extension in the freely moving intact crayfish *Cherax destructor.* 1. Activity of the tonic stretch receptor. *J. Exp. Biol.* **202:** 171–181.

McCarthy, B. J., and D. L. Macmillan. 1999b. Control of abdominal extension in the freely moving intact crayfish *Cherax destructor.* 11. Activity of the superficial extensor motor neurones. *J. Exp. Biol.* **202:** 183–191.

Patullo, B., Z. Faulkes, and D. L. Macmillan. 2001. The muscle receptor organs do not mediate load compensation during body roll and defence. *J. Exp. Zool.* (in press).

Paul, D. H. 1991. Pedigrees of neurobehavioral circuits: tracing the evolution of novel behaviors by comparing motor patterns, muscles, and neurons in members of related taxa. *Brain Behav. Evol.* **38:** 226–239.

Sokolove, P. G. 1973. Crayfish stretch receptor and motor unit behaviour during abdominal extensions. *J. Comp. Physiol.* **84:** 251–266.